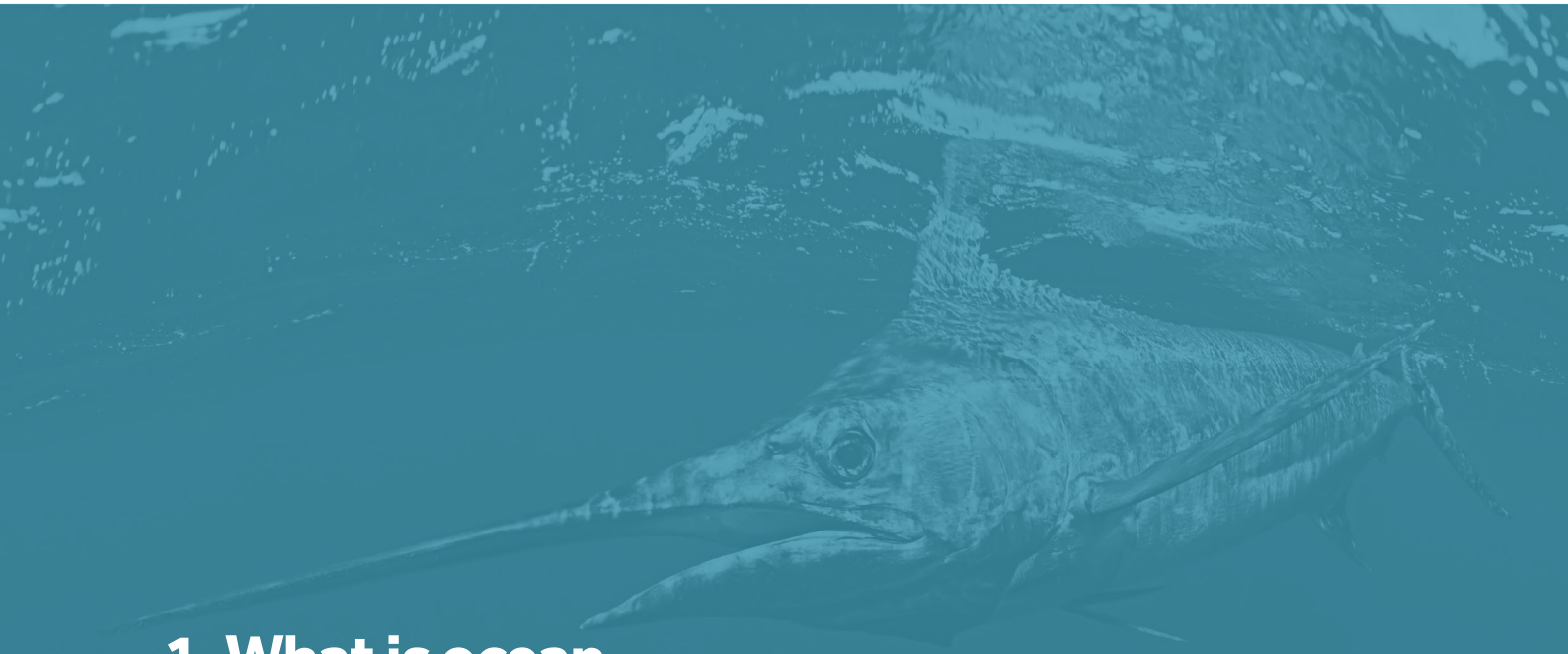
IUCN

Ocean deoxygenation: Everyone's problem

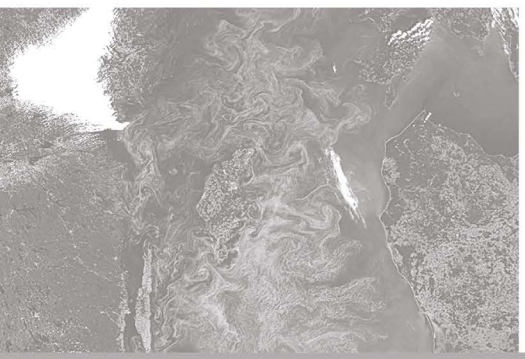
Causes, impacts, consequences and solutions

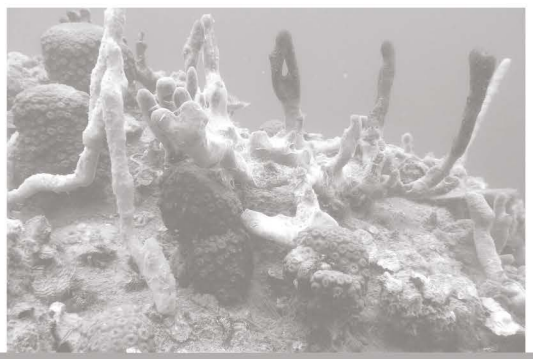
Edited by D. Laffoley and J.M. Baxter



1. What is ocean deoxygenation?

Marilaure Grégoire, Denis Gilbert, Andreas Oschlies and Kenneth Rose





IUCN GLOBAL MARINE AND POLAR PROGRAMME

WCPA WORLD COMMISSION ON PROTECTED AREAS

Government Offices of Sweden
Ministry of the Environment and Energy

United Nations Educational, Scientific and Cultural Organization · Intergovernmental Oceanographic Commission · Sustainable Development Goals

What is ocean deoxygenation?

1

Marilaure Grégoire[1], Denis Gilbert[2], Andreas Oschlies[3] and Kenneth Rose[4]

[1]Department of Astrophysics, Geophysics and Oceanography, MAST-FOCUS research group Université de Liège, 4000 Liège, Belgium.
[2]Maurice-Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, Québec, G5H 3Z4, Canada.
[3]GEOMAR, 24105 Kiel, Germany.
[4]University of Maryland Center for Environmental Science, Horn Point Laboratory, Cambridge, MD 21613, USA.

All the authors are members of the IOC-UNESCO Global Ocean Oxygen Network (GO_2NE).

Summary

- The equilibrium state of the ocean-atmosphere system has been perturbed these last few decades with the ocean becoming a source of oxygen for the atmosphere even though its oxygen inventory is only ~0.6% of that of the atmosphere. Different analyses conclude that the global ocean oxygen content has decreased by 1-2% since the middle of the 20th century. Global warming is expected to have contributed to this decrease, directly because the solubility of oxygen in warmer waters decreases, and indirectly through changes in the physical and biogeochemical dynamics.
- Since the middle of the 20th century, the increased river export of nitrogen and phosphorus has resulted in eutrophication in coastal areas world-wide. Eutrophication implies huge oxygen consumption, and when combined with a low ventilation, often due to vertical stratification, this leads to the occurrence of oxygen deficiencies near the sea bed. The number of reported sites affected by low oxygen conditions (>500) has dramatically increased in the last few decades. Climate warming is expected to exacerbate the decrease of oxygen by reducing the ventilation and extending the stratification period.
- The volume of anoxic zones has expanded since 1960 altering biogeochemical pathways by allowing processes that consume fixed nitrogen and release phosphate and iron, and possibly nitrous oxide (N_2O). The relatively small inventory of essential elements, like nitrogen and phosphorus, makes such alterations capable of perturbing the chemical composition equilibrium of the ocean. Positive feedback loops (e.g. remobilization of phosphorus and iron from sediment particles) may speed up the run away from this equilibrium in ways that we hardly know or understand.
- Deoxygenation affects many aspects of the ecosystem services provided by the ocean and coastal waters. For example, deoxygenation effects on fisheries include low oxygen affecting populations through reduced recruitment and population abundance, and also through altered spatial distributions of the harvested species causing changes in the dynamics of the fishing vessels. This can lead to changes in the profitability of the fisheries and can affect the interpretation of the monitoring data leading to misinformed management advice.
- Model simulations for the end of this century project a decrease of oxygen in the high and low emission scenarios, while the projections of river exports to the coastal ocean indicate that eutrophication will likely continue in many regions of the world. Warming is expected to further amplify the deoxygenation issue in coastal areas influenced by eutrophication by strengthening and extending the stratification.

Effects of low oxygen conditions	Potential Consequences
Reduction of the habitat available for pelagic, mesopelagic, and benthic organisms.	• Reduced growth and reproduction of aerobically-respiring organisms in regions with very low oxygen levels. • In extreme cases and for non-mobile species, low-O_2 induced mortality. • Cascading effects and alteration of the foodweb structure including the diversion of organic matter flow to low oxygen tolerant species like microbes. • In extreme cases, oxygen can become completely depleted and the waters become anoxic and even euxinic, in which only anaerobically respiring microbes can survive.
Reduction in the abundance and recruitment of fish populations.	• Alterations in the spatial distribution of harvested species. • Accumulation of species in well-oxygenated waters; these species may become more vulnerable to fishers targeting these high oxygen refuge areas. • Changes in the dynamics of the fishing vessels and in the profitability of the fisheries. • Affect the interpretation of the monitoring data leading to misinformed management advice.
Expansion of the volume of anoxic zones since 1960.	• Alteration of biogeochemical pathways of essential elements like nitrogen, phosphorus and iron. • Modification of the fixed nitrogen budget, with enhanced nitrogen fixation and denitrification but the balance of the two is not yet known. • Release of phosphate and iron from sediment particles and possibly nitrous oxide (N_2O). • Positive feedback loops may speed up the run away from equilibrium.
Challenges in model development and observation quality.	• Model development needs new observations and dedicated experiments (e. g. definition of critical thresholds for biogeochemistry and living species). • Model uncertainty. • Requirement for specific sensors for measuring ultra low oxygen conditions (at nM scale).

1.1 Introduction

During the Earth's history, the ocean has evolved through various oxidation states. The ocean was largely anoxic 3.85 billion years ago, mildly oxygenated in its upper layer up to 0.54 billion years ago and, finally, quite well oxygenated in its present state (Holland, 2006). Evidence is mounting that oxygen is declining in the modern ocean. Estimates are for a 1-2% decrease (i.e. 2.4-4.8 Pmol or 77-145 billion tons) of the global oxygen inventory since the middle of the last century (e.g. Bopp et al., 2013; Schmidtko et al., 2017). This results in modifications of the equilibrium state of the ocean-atmosphere coupled system with the ocean recently becoming a source of oxygen for the atmosphere. Regions with historically very low oxygen concentrations are expanding and new regions are now exhibiting low oxygen conditions. Schmidtko et al. (2017) estimate that the volume of anoxic waters worldwide has quadrupled since 1960.

While the importance of the different mechanisms responsible for the loss of the ocean oxygen content is uncertain, global warming is expected to contribute to this decrease, directly because the solubility of oxygen in warmer waters decreases, and indirectly through changes in ocean dynamics that reduce ocean ventilation. Today's processes are reminiscent of those thought to have promoted the occurrence of oceanic anoxic events (OAEs) that occurred episodically during the past several hundred million years and that led to major extinction events (Holland, 2006; Watson, 2016). While a full-scale OAE would take thousands of years to develop, the small oxygen inventory of the ocean (i.e. the oxygen inventory of the ocean is only ~0.6% of that of the atmosphere) makes it particularly sensitive to perturbations of its equilibrium oxidative state. The consequences of such perturbations on the biogeochemistry and ecosystem state are not well known.

The deoxygenation process is also affecting the estuary-coastal ocean continuum (referred as the coastal ocean throughout the following). The global increase of the nutrients exported by rivers from the land to the ocean and the resulting development of eutrophication in many hundreds of sites around the world has promoted algal productivity and the resulting over-consumption of oxygen in the bottom layer that is effectively isolated

through stratification from being replenished with the oxygen in the surface waters. Climate warming is expected to worsen the situation by further reducing the ventilation of bottom waters.

Deoxygenation in the global and coastal ocean will reduce the habitat available for pelagic, mesopelagic, and benthic organisms. In some regions, the oxygen level is so low that aerobically-respiring organisms can exhibit reduced growth and reproduction and, in extreme cases and for non-mobile species, experience low-O_2 induced mortality. The effects on individuals exposed to low oxygen can cascade and result in altered foodweb structure, including the diversion of organic matter flow to low oxygen tolerant species like microbes. In the case of anoxia and the eventual occurrence of sulphidic conditions, only anaerobically respiring microbes can survive. While the impact of low oxygen conditions on individual organisms can be investigated in laboratory experiments, the impact at the scale of the ecosystem, as well as on the goods and services delivered to humans, rely on field data and modelling and are more uncertain.

The transition towards anoxic conditions also affects important microbial and chemical processes governing the biogeochemical cycling of essential elements like nitrogen (N), phosphorus (P) and iron (Fe). Anoxic conditions halt nitrification and aerobic respiration and activate denitrification and the anaerobic ammonium oxidation (anammox) leading to a net loss of fixed nitrogen. On the other hand, nitrogen fixation is expected to be stimulated in waters with an excess of phosphorus over nitrogen; whether this can compensate for the loss of fixed nitrogen due to denitrification and anammox is uncertain.

The chemical composition of the ocean can be considered as fairly stable for the past several hundred millions of years (Watson et al., 2017), but the relatively small inventory of essential chemical elements (e.g. fixed N and P) makes them sensitive to relatively small perturbations. Perturbations of biogeochemical cycling of the order of those caused by deoxygenation have the potential to have significant effects on the biogeochemistry and resulting chemical composition on relatively short time scales of several thousands of years. Positive feedback loops like the remobilization of phosphorus and iron from sediment particles in low oxygen conditions can further accelerate the process by then stimulating primary production. In the geological past, perturbations of the phosphorus cycle drove the system away from equilibrium and promoted the occurrence of OAEs (Watson et al., 2017).

Model projections of the oxygen content of the ocean for the end of the 21st century show a decrease of oxygen under all current emission scenarios. Projections of river nutrients exports to the coastal ocean indicate that eutrophication will likely continue in many regions of the world and will be further amplified by warming acting to strengthen and extend stratification (Seitzinger et al., 2010).

1.2 Description of deoxygenation

The dynamics of oxygen in the ocean are governed by physical and biogeochemical processes. The ocean gains oxygen in the upper layer due to photosynthesis by autotrophic organisms and oxygen from the atmosphere dissolving in the under-saturated waters. Conversely, the ocean loses oxygen throughout the whole water column: at the surface, due to the outgassing of oxygen to the atmosphere in over-saturated waters, and from the surface to depths due to the respiration of aerobic organisms and oxidation of reduced chemical species. Evidence suggests that the global ocean oxygen inventory has been perturbed since the middle of the last century (Figure 1.1). We can assume that the oxygen produced by photosynthesis (i.e. net primary production) in the upper layer is roughly consumed by respiration within the water column, except for a small production of 0.002 Pmol O_2 yr^{-1} that corresponds to burial (Wallmann, 2000). An oxygen loss ranging from 0.048 Pmol O_2 yr^{-1} (Manning & Keeling, 2006) to 0.096 Pmol O_2 yr^{-1} (Schmidtko et al., 2017) results from a modification of the balance in the atmosphere-ocean fluxes with a decreasing influx from the atmosphere to the ocean and an increasing outflux from the ocean (e.g. Bopp et al., 2002; Frölicher et al., 2009). The lack of observations with sufficient resolution of sampling in space and time limits the rigour of our oxygen budget for the coastal zone.

1.2.1 Ventilation mechanisms

The surface mixed layer is well oxygenated in most of the ocean by photosynthesis and dissolution of atmospheric oxygen. But below the sunlit surface layer, there is no photosynthesis, so that the renewal of the oxygen consumed requires the existence of a physical mechanism that transports well-oxygenated waters

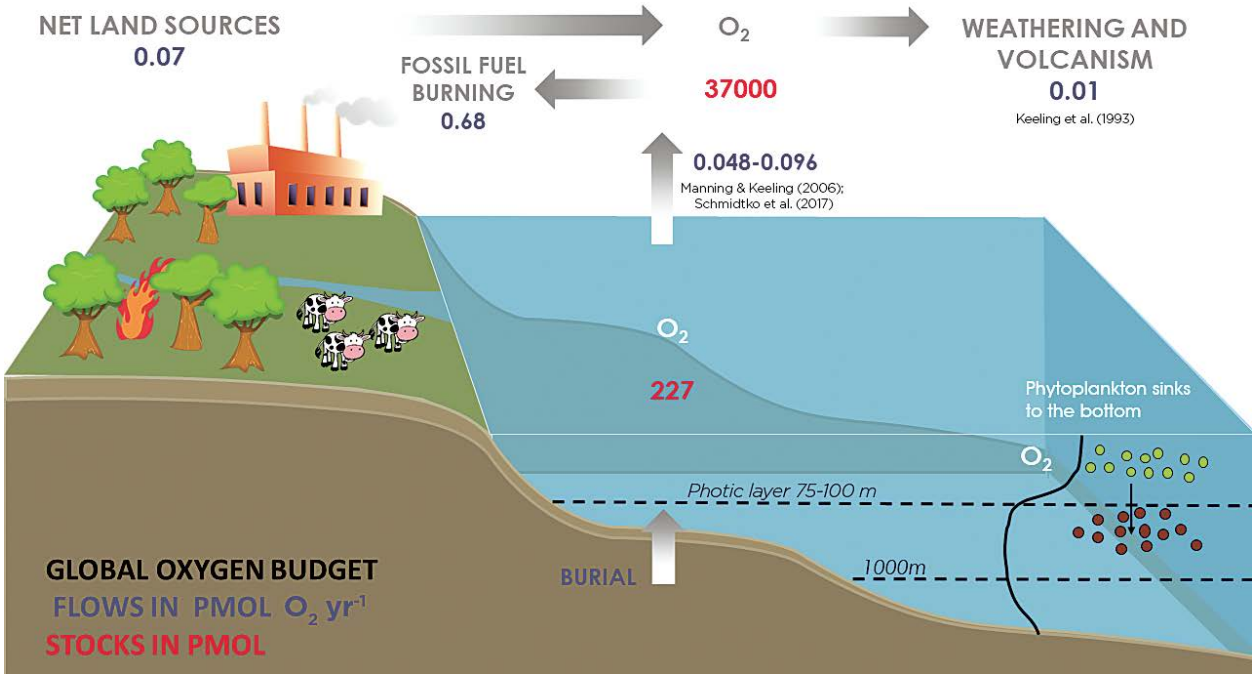


Figure 1.1 Tentative oxygen budget for the Ocean-Atmosphere system for the period 1960-2014. The stocks are in Pmol (for the Ocean from Schmidtko et al. (2017); for the atmosphere from Keeling et al. (1993)) while the fluxes are in Pmol O_2 yr^{-1}.
Globally the amount of oxygen produced by photosynthesis (estimated as the Net Primary Production, NPP from Bopp et al. (2013)) is compensated by the amount respired for the degradation except for a small burial that results in a net production of oxygen of 0.002 Pmol O_2 yr^{-1}. The net air-sea oxygen flux is directed to the atmosphere and its range has been estimated from (lower value) Manning and Keeling (2006) (for 1993-2003) and (higher value) from Schmidtko et al. (2017) (for the last 50 years).
For the atmosphere, the oxygen consumed by the combustion of fuels and industry, land-use change as well as the net oxygen produced by the biosphere has been computed using the averaged estimates (over 1960-2014) from the global carbon project (Le Quéré et al., 2015) using the O_2:C ratios from Keeling and Manning (2014).

to the low oxygen waters. This mechanism, called ocean ventilation, is responsible for the oxygenation of deep and intermediate ocean waters and modifies the spatial distribution of oxygen within the ocean. The intensity of ocean ventilation strongly varies vertically and horizontally and over time. In the coastal ocean, ventilation of bottom waters results from advection from offshore, and mixing processes from surface cooling and wind mixing and in some areas tidal action and flushing events from the rivers.

In the global ocean the main ventilation mechanisms and pathways are as follows:

- Waters of a given density, an isopycnal, within the permanent thermocline (i.e. layer of significant temperature gradient) of the subtropical gyres are ventilated at the latitude where that isopycnal intersects the base of the surface mixed layer during the winter. At the end of each winter, waters near the base of the mixed layer subduct into the ocean interior, and then begin to slowly diffuse equatorward. This ventilation process is particularly intense at the high latitude end of the subtropical gyres, where subtropical mode water (STMW) is formed (Figure 1.2). This process ventilates subtropical gyres to depths of about 500 to 900 m.
- In the Southern Ocean, a surface convergence zone between about 50°S and 60°S causes local water to sink and the formation of Antarctic Intermediate Water (AAIW) which ventilates water depths between about 700 and 1200 m. The Southern Ocean is also home to the formation of the densest waters of the world ocean, Antarctic Bottom Waters (AABW), formed in areas of intense sea ice freezing and brine rejection around the continent of Antarctica. These waters sink all the way to the bottom of the three major ocean basins and propagate northward (Figure 1.2).
- In the northern hemisphere, ventilation processes vary quite a lot between the major ocean basins. In the North Atlantic, to the north of the Denmark-Faroe-Shetland ridge, deep convection in the Greenland-Iceland-Norwegian Sea (GINSEA) is

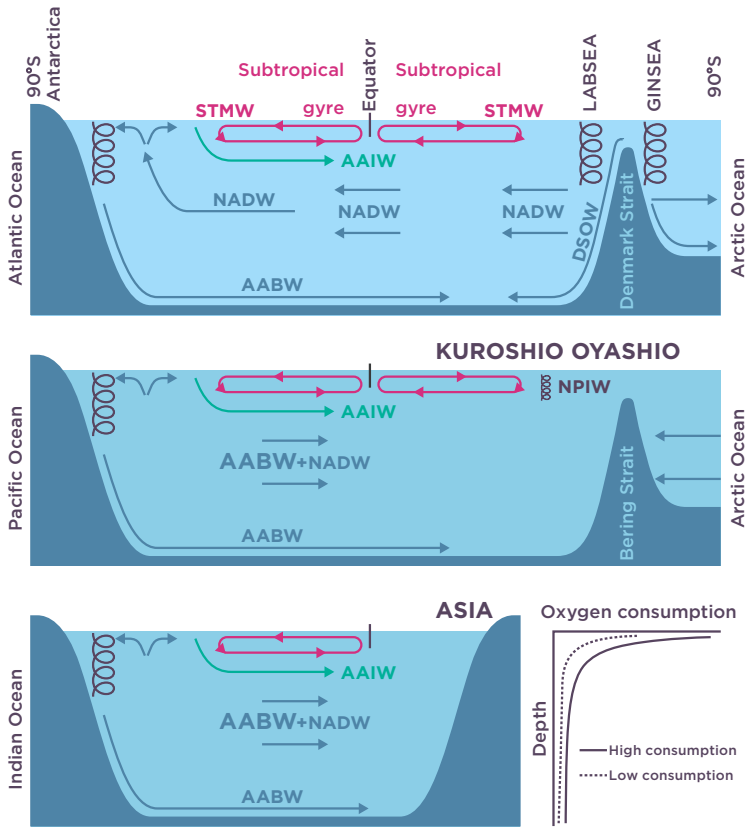


Figure 1.2 Meridionally averaged view of ventilation in the global ocean. STMW: Subtropical Mode Water, AABW: Antarctic Bottom Waters, AAIW: Antarctic Intermediate Waters, DSOW: Denmark Strait Overflow Water, NADW: North Atlantic Deep Water, NPIW: North Pacific Intermediate Waters, LABSEA: Labrador Sea, GINSEA: Greenland-Iceland-Norwegian Sea.

the source of Denmark Strait Overflow Water (DSOW) that spills over the Denmark Strait sill (625 m deep) and then descends to the bottom of the North Atlantic. Some of this dense water also flows northward and propagates towards the Arctic Ocean. The Labrador Sea, and to a lesser extent the Irminger Sea, is another important site of deep-water formation in the North Atlantic, with convection events reaching up to 2000 m depth. This leads to the formation of North Atlantic Deep Water (NADW) which then propagates southward. The ultimate fate of NADW is to either i) upwell into a surface divergence zone of the Antarctic Circumpolar Current; ii) ventilate the Indian Ocean; or iii) ventilate the Pacific Ocean (Figure 1.2).

- During the very long journey from its formation region in the northern North Atlantic, NADW remains isolated from the atmosphere and its oxygen content becomes progressively lower as it gets further away from its source region. In the Indian and Pacific Oceans, a mixture of NADW and predominantly AABW (Johnson, 2008) propagates northwards. No deep-water formation takes place in the Pacific and Indian Oceans, so that they are less well ventilated than the North Atlantic (Figure 1.2) and have lower oxygen content. The formation of North Pacific Intermediate Water (NPIW) in the mixed water region of the Oyashio (i.e. cold current flowing south-westward from Kamchatka to Japan) and Kuroshio (i.e. warm current flowing northward from Taiwan to Japan) ventilates the upper 300 to 700 metres of the North Pacific subpolar gyre (Talley, 1993).

Projections from Earth System Models that simulate global warming from rising CO_2 levels indicate that ventilation processes will likely become more sluggish in the next decades (Bopp et al., 2013). An analysis of oxygen data from the global ocean tentatively suggests that such reduced ventilation may already be underway (Schmidtko et al., 2017). But large interdecadal variability is present, causing us to remain prudent in this conclusion. For instance, records preserved in the sediments underlying Oxygen Minimum Zones (OMZs) show that the rate of ventilation changes on multiple time scales. Climatic phenomena like El Niño, the Pacific Decadal Oscillation (PDO) and Ice Ages all change the rate at which the deep ocean gets replenished with

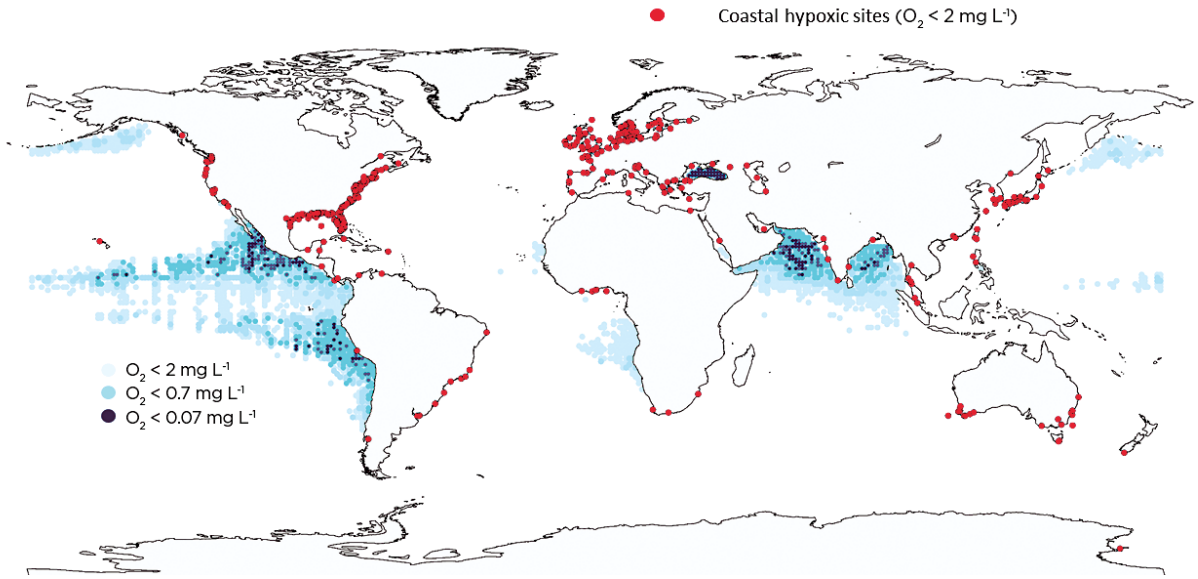


Figure 1.3 Global distribution of deoxygenation in the coastal and global ocean (from Breitburg et al., 2018). In the coastal area, more than 500 sites have been inventoried with low oxygen conditions while in the open ocean the extent of low oxygen waters amounts to several millions km^3.

oxygen. In the north Pacific Ocean, Deutsch et al. (2014) have found that the variability over the last 150 years of the extent of the anoxic zone responds to the variability of the trade winds intensity that impacts on the thermocline depth and hence on the level of respiration (i.e. a shallower thermocline is expected to be associated to higher reparation rates). For most of the 20th century up to 1990, they found that the thermocline depth increased in answer to the weakening of the intensity of the tropical trade winds and this reduced the respiration demand and anoxia extent. The long-term variability of the extent of OMZ and, in particular of their anoxic part, results from the interplay of wind-driven and stratification-driven effects but the relative influence of these effects is not yet known (Deutsch et al., 2014).

During the last glacial termination (from 20 000 to 10 000 BP), the upper ocean generally became less oxygenated while the deep ocean became more oxygenated. All these changes are driven by a subtle balance between decreased oxygen solubility due to warming, increased ventilation of the abyssal ocean, shift of organic matter respiration rates from the deep to the upper ocean, and possibly a global reduction of respiration due to nutrient inventory (Jaccard & Gallbraith, 2012).

1.2.2 Formation of a Low Oxygen Zone (LOZ)

The oxygen concentration realized in waters below the surface layer results from the equilibrium between its consumption via oxygenated respiration and its renewal by ocean circulation. Oxygen consumption processes (animal respiration, bacterial degradation of organic matter) remove oxygen from the water column. In the global ocean, the rate of oxygen consumption is greatest near the ocean surface and decreases exponentially with depth (Figure 1.2). Most of the respiration of the exported production occurs in intermediary waters, between 100-1000 m, and the fraction of organic matter that reaches waters below 2000 m is rather small. Any modification of this organic matter flux is expected to impact on the vertical distribution of oxygen and oxygen content of the deeper waters. In the coastal ocean, a significant part of the surface primary production reaches the bottom layer where it is degraded with possibly high oxygen consumption rates in the sediment.

Some regions of the global and coastal ocean below the surface are permanently poorly ventilated (e.g. intermediate waters of some regions of the tropical ocean) or periodically ventilated (e.g. bottom waters in coastal systems). In these regions, the oxygen concentration reaches such low values that it alters the ecosystem and biogeochemical cycles. These regions are considered as Low Oxygen Zones (LOZs) and, for the global ocean, they are frequently named Oxygen Minimum Zones (OMZs). The thresholds below which the oxygen deficiency has biological and biogeochemical impacts differ in terms of values and reporting units. For the biogeochemistry, it is the absence of oxygen that alters the biogeochemical cycling of N, P and Fe. The oxygen concentration threshold for impacts on living

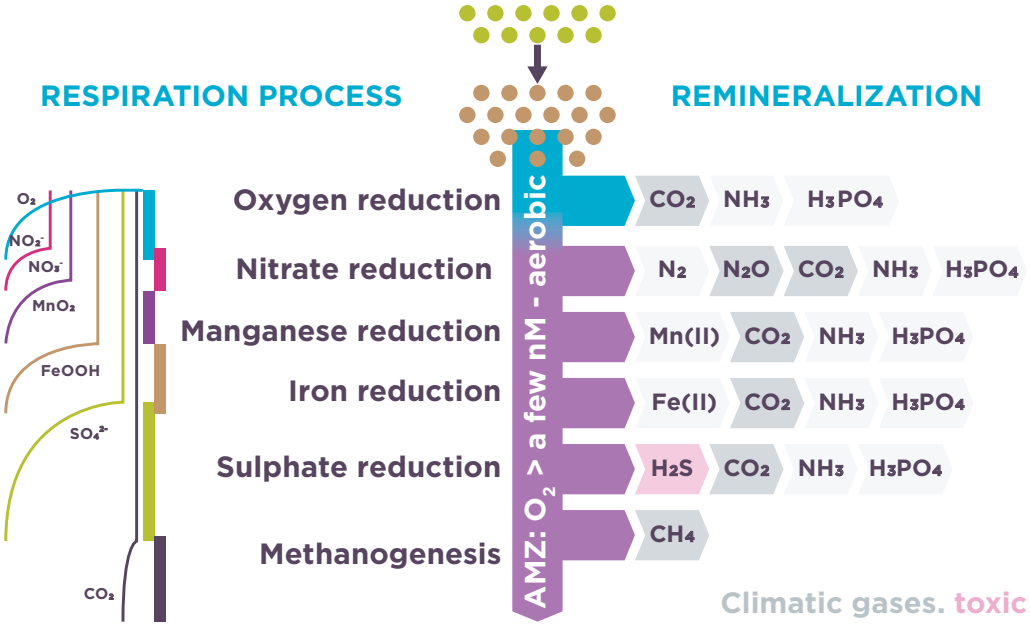


Figure 1.4 Succession of respiration processes in oxic and anoxic environments. In oxygenated waters, only oxic respiration occurs while in anoxic regions there is successively nitrate reduction (i.e. denitrification), manganese, iron, sulphate reduction and finally methanogenesis (Figure modified from Canfield & Thamdrup, 2009).

organisms varies somewhat across taxa. The definition of LOZs is based on fixed threshold values, with about 20 µmol O_2 kg^{-1} (i.e. ~5% saturation) for OMZs and about 61 µmol O_2 kg^{-1} for coastal LOZs. In extreme cases, oxygen can become completely depleted and the waters become anoxic and even euxinic when hydrogen sulphide, a toxic compound for most marine life (except some forms of bacteria), is produced.

1.3 Global / Regional differences in mechanisms

LOZs can be found in different ecosystems encompassing the open ocean, (semi)-enclosed seas, the estuary-coastal ocean continuum up to the edge of the continental shelf, and upwelling margins (Figure 1.3). The basic mechanisms responsible for the formation of low oxygen conditions differ across systems (e.g. Fennel & Testa, 2018). The configuration of the basin (e.g. open versus (semi)-enclosed), its bathymetry, and specifics of the land-sea-sediment-atmosphere interactions determine the residence time of waters and the level of biological production and hence the system's sensitivity to deoxygenation. Basically, low oxygen conditions naturally exist in the open ocean in regions without unusually high rates of O_2 utilization, but where the circulation is most sluggish and ventilation times are longest. The most poorly ventilated waters are found in the subsurface layers (~100 - 1000 m) of the Tropical Ocean inside relatively stagnant cyclonic gyres that exist north and south of the equator in the eastern part of ocean basins (Karstensen et al., 2008). These OMZs are permanent features, but their upper boundaries are highly dynamic, and the analysis of long time series data have shown that their upper boundary is extending upward (Stramma et al., 2008). In some parts of the Eastern Tropical Pacific, recent observations made with sensors with detection limits of a few nM reveal the presence of an Anoxic Marine Zone (AMZ) between 100 - 500 m inside the OMZs (Tiano et al., 2014). The absence of oxygen in these AMZs gives rise to peculiar microbial processes (Figure 1.4) that are described below.

Similarly, naturally poor ventilation due to restricted vertical circulation explains the deficiency of oxygen in some enclosed basins, such as the Baltic and Black Seas. In areas, like the Black Sea and the Cariaco basin, the degradation of organic matter leads to the production of a huge pool of hydrogen sulphide, a compound that is toxic for most animal life. In the Black Sea case, the opening of the Bosphorus strait ~10 000 years ago, and the resulting intrusion of the salty Mediterranean waters, transformed the basin from a lake to the largest euxinic region ($4.7x10^5$ km^3 of sulphidic waters) in the world. Few aerobically-respiring animals are found in the waters between 100 m depth and the bottom.

The eastern branch of the main anti-cyclonic gyres located in both hemispheres in the Atlantic and Pacific Oceans leads to the occurrence of major upwelling zones along the eastern boundary of the ocean, i.e. Eastern Boundary Upwelling Systems (EBUS). These upwelling zones are located off Peru-Chile, Namibia, California and Senegal. They bring oxygen depleted and high nutrient waters from the open ocean OMZs onto the continental shelf. These upwelling zones have high levels of primary and secondary production that biologically support many of the world's important fisheries. They have very high oxygen consumption rates, and this is where the most intense and thick OMZs tend to be found. The degradation of the organic material consumes unusually large amounts of oxygen and can generate severe hypoxia and even anoxia with potential detrimental consequences for aerobically respiring living organisms. The variability of the oxygen conditions in EBUS depends on the intricate interplay between local (e.g. local wind mixing versus stratification) and remote (e.g. equatorial current) forcing. These, in turn, affect the ventilation mechanisms, the productivity of the region and the intensity of the upwelling (e.g. Bachèlery et al., 2015; Bettencourt et al., 2015).

The open ocean OMZs are naturally poorly ventilated and climate change is expected to further lower ventilation. For instance, in the Black Sea, the depth of the oxygenated layer has dramatically decreased from 140 m in 1955 to 90 m in 2015 (Figure 1.5) very likely due to the reduced formation of well oxygenated waters in winter (Capet et al., 2016).

In parallel with the expansion of these naturally occurring oxygen deficient areas, anthropogenically-induced LOZs have also been rapidly increasing (Diaz & Rosenberg, 2008) (Figure 1.6). After the 1950s, the Haber-Bosh process offered a way to synthetically fix N to form ammonia at an industrial scale. This process has allowed for the mass production of synthetic fertilizers. The Haber-Bosh discovery and the increasing burning of fossil fuels have led to anthropogenic sources of newly created fixed N becoming two to three times larger than natural terrestrial sources resulting in substantial changes in the N cycle (Galloway et al., 2013). For coastal areas with large river inputs, it resulted in an increase in the delivery of fixed N by ~30 % from 1970 to 2000 (Seitzinger et al., 2010). Similarly, over the same period, dissolved inorganic phosphorus also increased by ~30%. This influx of nutrients leads to the eutrophication (over-enrichment) of the waters in the coastal zone. Eutrophication stimulates primary production and, to some extent, can be beneficial to fisheries. But if not well managed, eutrophication may

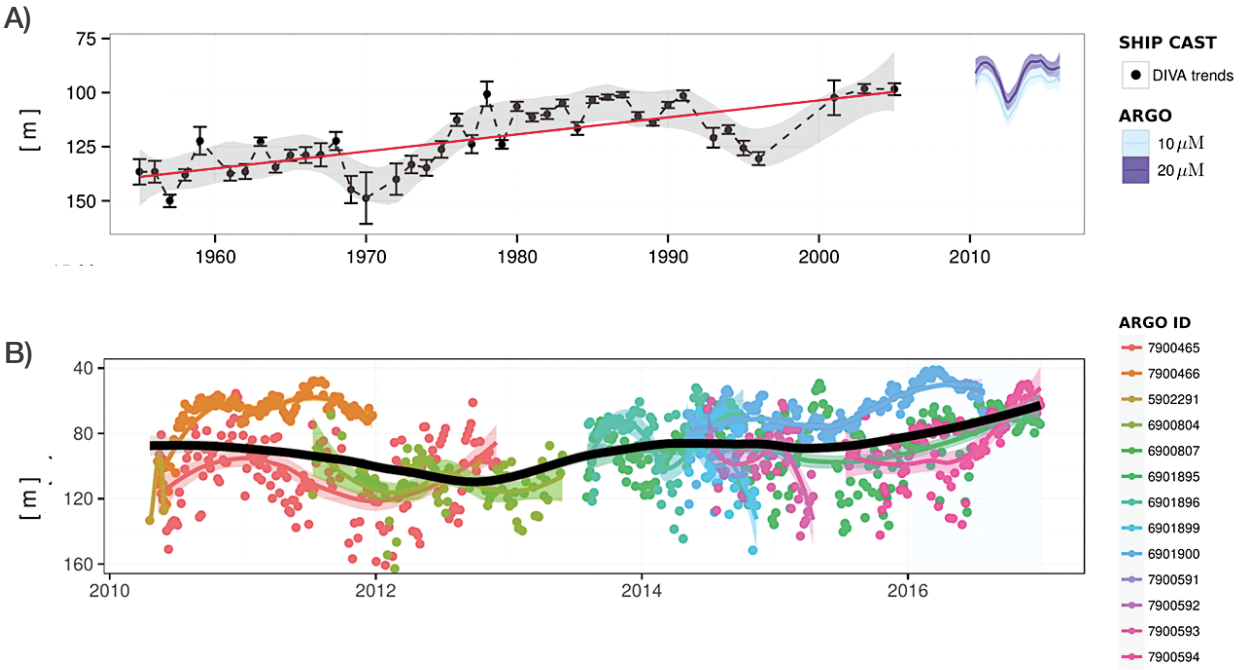


Figure 1.5 The surface oxygenated layer of the Black Sea has been shrinking from 140 m in 1955, 90 m in 2010-2015 and 72 m in 2016. A) trends of oxygen penetration depth deduced from (dots) the analysis of ship-based casts and (blue) ARGO floats. B) trend reconstructed from Argo floats over 2010-2016 (Figure from Capet et al., 2016).

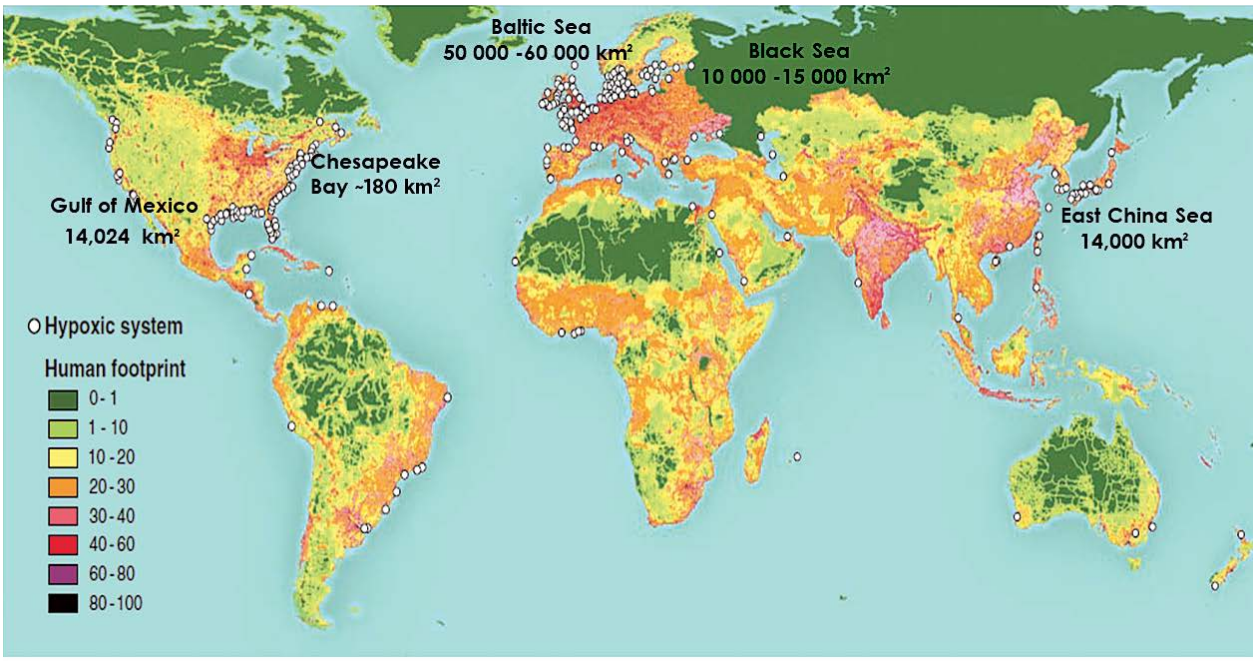


Figure 1.6 Global distribution of systems that have been reported as eutrophication (N and P enrichments)-associated LOZs. Their distribution matches the global human footprint (the normalized human influence is expressed as a percentage) in the Northern Hemisphere. For the Southern Hemisphere, the occurrence of dead zones is only recently being reported. Affected water bodies range from small coastal lagoons to large systems like the Baltic Sea, Black Sea, Kattegat, and East China Sea, and the Northern Gulf of Mexico. It should be noted that low oxygen zones can only be detected where monitoring is in place, and the uneven efforts in monitoring and research may contribute to the much higher number of low oxygen areas reported in the northern hemisphere (Figure from Diaz & Rosenberg, 2008).

lead to massive development of algae that produce large amounts of organic material that sink to the sea bed. When bottom waters are not well ventilated (e.g. in periods of vertical stratification), the oxygen consumed cannot be replaced and this leads to the creation of a LOZ. Coastal LOZs result from excessive external nutrients inputs from the rivers and once established, they are further stimulated by internal nutrients sources activated by the deoxygenation process (Figure 1.7). Indeed, the remobilization of bound P from the sediments in anoxic conditions will further aggravate the deoxygenation process by releasing P that further stimulates primary production. Even after a reduction of river nutrients, coastal systems require several years to recover because the sediment continues to consume large amounts of oxygen and can continue to leach out nutrients that accumulated during eutrophication (Conley et al., 2009).

1.4 Trends and impacts

1.4.1 Observations

The advent of autonomous platforms like Argo floats (Figure 1.8) and (wave) gliders has the potential to boost our knowledge of oxygen dynamics at the mesoscale and even sub-mesoscale (1 to 100 km) (e.g. Pascual et al., 2017). Up to now, more than 100 000 oxygen profiles have been collected by Argo floats throughout the ocean, allowing depiction of the oxygen patterns over large areas. The inclusion of Argo oxygen data in global climatologies and trend estimation is promising but has not been done so far because of oxygen sensor calibration and data management issues.

Oxygen measurements at the very low concentrations (< 5 µmol O_2 kg^{-1}) found in some parts of LOZs are technically challenging and the historical data at very low oxygen concentrations have been often suspect (Bianchi et al., 2012). Consequently, estimation of the extent and evolution of OMZs with particularly low oxygen concentrations at their core (e.g. AMZs) are still uncertain. Recent oxygen sensors with detection limits as low as a few nanomoles are now available and have changed our view of the biogeochemistry of OMZs (Tiano et al., 2014). The emergence of these new platforms and sensors makes possible the implementation of regional and global oxygen observatories targeted towards the monitoring and management of the deoxygenation process.

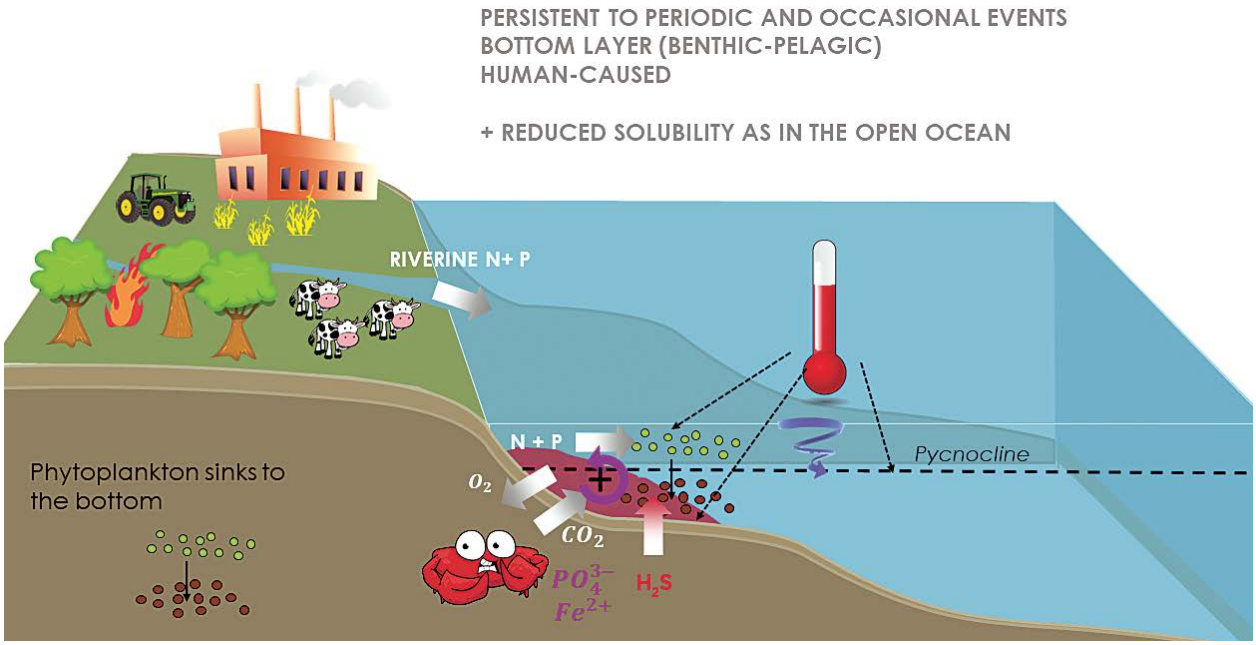


Figure 1.7 Schematic of the generation of a LOZ in the coastal area. Large nutrients discharges from the rivers stimulate intense primary production that sinks to the bottom where it is degraded consuming large amounts of oxygen. When the ventilation is not able to renew the oxygen consumed, a LOZ is generated and in extreme cases hydrogen sulphide escapes the sediment. Low oxygen conditions in bottom waters enhance the release of inorganic phosphorus that will stimulate primary production and hence feedbacks positively on the oxygen depletion.

Table 1.1 Oxygen Content and change per basin for the main areas affected by deoxygenation. Synthesis of the information provided by Schmidtko et al. (2017)

Basin	Oxygen decrease since 1960 (Pmol)	Change as percentage of global change (%)	Decrease as percentage of basin change since 1960 (%)	Causes
Global ocean	4.8 ± 2.1			Up to 1000 m: solubility plays a major role and explains 50% of the oxygen loss. Below 1000 m: changes in deep water formation and thermohaline circulation with natural variability superimposed are suggested to explain the oxygen loss.
North and Equatorial Pacific Ocean	1.9 ± 0.8	39.9 ± 17.2	3.8	Upper Layer: decline in the formation rates of North Pacific Intermediate waters due to warming changes on the time scales of Pacific Decadal Oscillation (PDO) are observed Below 1000 m: no impact of PDO has been found
Southern Ocean	0.8 ± 0.2	15.8 ± 4.9	2.1	Decline in deep water formation of Antarctic water masses due to changes in thermal buoyancy and in circumpolar wind patterns. Most pronounced in the Indian and Pacific sectors in parallel to the increase of salinity and temperature of the Antarctic Bottom Water of the circumpolar deep water.
South Atlantic Ocean	0.6 ± 0.1	12.4 ± 2.8	2.7	Reduced ventilation due to meridional overturning changes affect mainly the entire deep water column between north Atlantic deep water and Antarctic bottom water. Multi decadal variability.
Arctic Ocean	0.36 ± 0.15	7.6 ± 3.1	7.8	Reduced deep water ventilation due to a freshening and warming in the Canada Basin and Beaufort Sea. Increased consumption by enhanced biological activity due to sea ice reduction in summer.

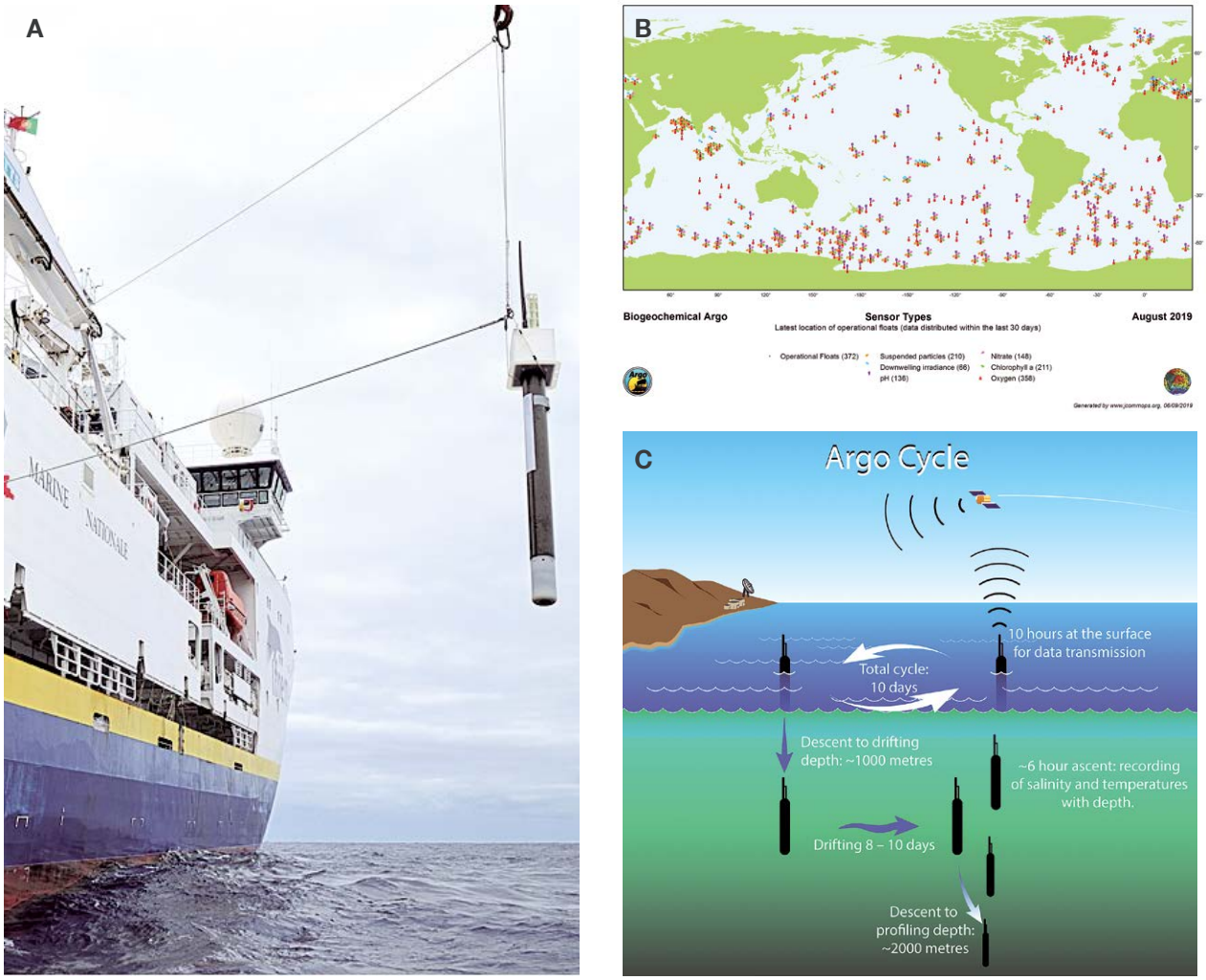


Figure 1.8 A) Deployment of an ARVOR float from the French R/V Pourquoi Pas; B) position of biogeochemical Argo floats in August 2019; C) schematics of an Argo profile cycle (sources: Map JCOMMOPS; photos : http://www.argo.ucsd.edu/pictures.html with courtesy of John Garrett, Skeptical Science for the Argo cycle).

1.4.2 Trends

Since the middle of the 20th century, the global and coastal ocean have had to face deoxygenation. In the global ocean, the oxygen content is decreasing and OMZs are expanding while in the coastal ocean, the occurrence of bottom LOZs is more and more reported.

Evidence shows that the oxygen balance in the global ocean has been perturbed during the last decades with the consequence that the oxygen inventory is globally decreasing (e.g. IPCC, 2013; Ito et al., 2017; Schmidtko et al., 2017; Stramma et al., 2008). Observations and model simulations agree that the ocean oxygen content has decreased by 1-2% since 1960. This decrease is not uniform but rather varies across ocean basins and depths (Table 1.1). The largest loss is observed at the depth of the main thermocline between 100-300 m in the Tropical and North Pacific Ocean, the Southern and Arctic Ocean and the South Atlantic Ocean (Table 1.1).

Natural climate fluctuations can substantially contribute to the interannual to decadal variation in oxygen and can preclude unequivocal detection of any climate driven signal. This is particularly the case for the North Atlantic and North Pacific regions where the surface and subsurface oxygen concentrations are statistically linked with the North Atlantic Oscillations (NAO) and Pacific Decadal Oscillations (PDO) climate modes (Andrews et al., 2013; Duteil et al., 2018; Frölicher et al., 2009). Volcanic eruptions are another natural forcing that is superimposed onto the anthropogenic and internal drivers that govern oxygen variability. Volcanic eruptions enhance the amount of oxygen taken up by the ocean due to a cooling effect that reduces the stratification and increases solubility. The oxygen

inventory increases globally in the top 500 m, and this increase compensates for part of the human-induced decreasing trend in oxygen that follows an eruption (Frölicher et al., 2009). The identification of the causes of deoxygenation requires extracting the climate signal from the natural and internal variability of the ocean system. Models, supported by observational data, are essential for making this differentiation as, currently, the available observations alone do not allow sufficient differentiation of the different contributing drivers and signals.

Global warming is expected to further decrease the global ocean oxygen content directly because the solubility of oxygen is lower in warmer water (i.e. direct thermal effect) and indirectly through changes in ocean dynamics (e.g. increased stratification, decreased mixing layer subduction, convective mixing and deep-water formation, slowdown of the thermohaline circulation) that reduce ocean ventilation. These changes have affected the balance of the air-sea oxygen flux, reducing the amount of oxygen that goes from the atmosphere to the ocean and increasing the outgassing of oxygen from the ocean. A reduction of deep-water formation will affect the whole ocean after decades to hundreds of years (dependent on depth). These changes may also have an impact on key biogeochemical processes and hence the local production-consumption of oxygen in a way that is still not clearly understood. For the same level of global photosynthesis and respiration, the increased stratification reinforces the decoupling between the oxygen oversaturated surface waters and the undersaturated subsurface waters. This strengthened decoupling increases the outgassing of oxygen. Observations and modelling have been combined in order to determine the relative importance of these different mechanisms and how they have affected the oxygen dynamics of different ocean basins. Clearly, the different layers of the ocean respond to global warming with different time scales; the surface layer responding after just a few years, whilst the intermediate layers and the deep ocean adjust to surface conditions on 10 to 120 years (Karstensen et al., 2008) and millennial time scales, respectively. In addition, the mechanisms of deoxygenation differ regionally and in particular differ vertically within a system. Over the first 1000 m of the water column, ~50% of the oxygen loss can be attributed to solubility change, while below 1000 m, changes in ocean circulation and deep-water formations with natural variability superimposed explain the oxygen loss. Globally, it has been shown that the direct thermal effect can only explain a limited fraction (~15%) of the oxygen decrease observed globally; the remaining part being imparted to indirect effects (Schmidtko et al., 2017).

Diaz and Rosenberg (2008) classified systems affected by oxygen deficiency according to the frequency of occurrence and duration of their low oxygen events. They found that since the 1960s the number of reported coastal LOZs has approximately doubled every ten years from ~25 in 1960 up to ~400 in 2007. Coastal LOZs exhibit different types of dynamics in response to the local aspects of primary production, stratification and mixing. Episodic events, with infrequent oxygen depletion (i.e. less than one event per year as defined by Diaz and Rosenberg, 2008), represent ~17% of the reported coastal LOZs and are the first signal that a region may potentially be shifting towards higher frequency oxygen deficiency. In small systems (e.g. river-estuary, bay, lagoon, inlet), oxygen depletion may appear several times per year lasting from a few hours to days or weeks. In these systems (~25%), local weather events and the periodic spring-neap-tidal cycles govern the variability of the primary production and the alternation between stratification and mixing periods. Low oxygen in about 50% of the reported LOZs occurs seasonally in summer-autumn when the seasonal thermocline or pycnocline is established and prevents the ventilation of bottom waters. The oxygen consumed by the degradation of the spring algal bloom cannot be replaced and a LOZ is generated in the benthic boundary layer. In systems prone to permanent stratification (8%), a persistent LOZ develops.

1.4.3 Projecting deoxygenation

Robust model projections under various scenarios of changes are needed for the global and coastal ocean in order to test in advance the potential impacts of mitigation strategies. The projection and forecasting of deoxygenation are based on state-of-the-art models that couple the physics and biogeochemistry, interact with the atmosphere and, in the coastal ocean, are linked with the land and the sediments. Mechanistic models are powerful tools to understand the underlying processes operating and to be able to then differentiate the causes of the oxygen decrease. While models used for projecting deoxygenation in the global and coastal ocean are quite similar in terms of formulations, their resolution in space and time, required accuracy, horizon of projections, and scenarios differ. A climate approach, with long term projections up to the end of the 21st century under global change scenarios, is needed for

the global ocean. Conversely, for the coastal ocean, a weather-based approach with medium to short term projections and forecasting is more appropriate: medium term projections (< 20 years) can support the implementation of regional river nutrients management strategies while, the setting up of a warning system, would require the implementation of an operational framework delivering near real time forecasts with a high accuracy.

Global models are able to reproduce the observed decline in the global oceanic oxygen inventory since 1960. Yet, they are not able to represent the spatial (region-specific) patterns of decrease and, in particular, the observed decline in the tropical thermocline. For the 21st century, an ensemble of models consistently predicts that continued global warming will worsen deoxygenation in the surface and deep ocean under the high mitigation (RCP 2.6) and business as usual (RCP 8.5) scenarios, with decrease of the global oxygen inventory of 1.81 ± 0.31 and 3.45 ± 0.44% , respectively (Bopp et al., 2013). Yet, there is still little agreement in the simulated spatial distribution of low oxygen areas with concentrations less than 100 µmol O_2 kg^{-1} (Cabre et al., 2015). This uncertainty limits our ability to reliably predict the impact of climate warming on the open-ocean OMZs and hence on oxygen sensitive biogeochemical processes including the N budget. The predictive skill of coarse resolution ocean models at low latitudes is limited by the need to resolve zonal currents thought to be important in supplying oxygen into the tropical OMZs (Brandt et al., 2010; Keeling et al., 2010; Stramma et al., 2010).

Looking at a longer time horizon; by 2150, the decreasing oxygen trend projected up to 2100 for the tropical intermediate (200-1000 m) reverses. The volume of OMZ is projected to shrink through 2300 with consequences on the N budget through a reduction of denitrification. This may potentially have important climate feedbacks through the reduced production and emission of N_2O to the atmosphere (Fu et al., 2018). Model simulations show that the causes for this oxygen increase are a reduction of export production combined with an intensified ventilation after 2200. Fu et al. (2018) suggest that at the end of the 21st century the projected expanding tropical OMZs do not reach a steady state but rather are in transition towards volume reduction.

Projecting oxygen levels in individual coastal water bodies requires modelling the variability of the ventilation and primary production from hours to weeks in response to changing river discharges (e.g. fresh water, inorganic nutrients, suspended particles), local weather conditions (e.g. wind storms, flooding events, heat waves), interactions with offshore (e.g. advection, upwelling), oxygen consumption in the sediments, and possibly the influence of the spring-neap tidal cycle. Coastal and regional models have the ability to represent the oxygen dynamics at monthly to weekly time scales but their performances can be hampered by the quality of their boundary conditions, mainly river discharges and atmospheric forcing that do not have the required spatial and temporal resolutions. Coastal models are progressively evolving towards a structure that allows a seamless coupling of the river-estuary-coastal ocean continuum. This will offer an improved quantification of the export of nutrients, and, in particular of N and P, along the river-ocean dimension.

The mitigation of coastal deoxygenation requires the implementation of effective nutrient reduction strategies based on a dual reduction of N and P to control the level of eutrophication (Conley et al., 2009). The economic costs associated with the reduction of anthropogenic nutrients is substantial and thus it is crucial that the level of reduction in a given coastal system be based on a deep comprehension of the processes governing oxygen dynamics and the likely ecological benefits. Over the last decades, regional action plans have been implemented in order to reduce the amount of nutrients discharged to the coastal zone through better wastewater treatment and other best management practices. However, to date, the positive effects are not always as expected and some regions remain far from reaching their nutrient reduction targets as positive feedback mechanisms (i.e. enhanced release of iron-bound phosphate in low oxygen conditions) and sediment inertia continue to emit nutrients for several years after reduction (e.g. Capet et al., 2013; Conley, 2012; Rabalais et al., 2010). Even when the nutrients level returns to a reference state, some systems may not return to their initial reference but rather may go to a new ecological state due to the non-linearity of living systems (Duarte et al., 2009).

Nutrient management in agriculture, the reduction of P detergent, and the increasing connections of people to sewage plants with high levels of treatment will control the amount of river export of fixed N and dissolved inorganic P (Seitzinger et al., 2010). Based on four scenarios of socio-economic development and using

an indicator of coastal eutrophication potential (Billen & Garnier, 2007), Seitzinger et al. (2010) estimate that risk for coastal eutrophication in many regions of the world until at least 2030 will likely continue due to the increase in inorganic P and N and changes in the nutrient ratios of river exports. Warming is expected to further exacerbate the deoxygenation issue by intensifying respiration and reducing the ventilation process due to a reduced solubility and stronger, prolonged stratification.

1.4.4 Impacts

1.4.4.1 Impact on biogeochemistry and biogeochemical feedbacks

The transition to anaerobic conditions induces major changes in the biogeochemical cycling of essential elements like N, P and Fe in the water column and in the underlying sediments. Some of these modifications will further the deoxygenation process as positive feedback loops may establish and stimulate further oxygen consumption. Special microbial processes start to operate, such as anaerobic remineralization of organic matter by denitrification and anaerobic ammonium oxidation (anammox), leading to formation of dinitrogen gas N_2 (a component that is largely inaccessible for most organisms) and a net loss of bioavailable N in the ocean. Nitrous oxide (N_2O), a potent greenhouse gas, is formed as a byproduct during nitrification and as an intermediate product during denitrification (Bange, 2006). Because the oxygen thresholds that govern the microbial pathways to N_2O are not precisely known, the role of OMZs in the marine N_2O budget is debatable. In a warming world, the sign of change of the N_2O budget (e.g. Bianchi et al., 2012; Martinez et al., 2015) and the sign of the air-sea flux of N_2O are uncertain, as increased stratification is expected to prevent N_2O from reaching the surface ocean and escaping to the atmosphere (Martinez et al., 2015).

Estimates of the total loss of bioavailable N from the open ocean is currently estimated to be 0.005-0.006 Pmol N yr^{-1} from the water column, and 0.01-0.02 Pmol N yr^{-1} from sediments (Somes et al., 2013). Analysis and modelling of global benthic data also indicate that denitrification in sediments underlying high nutrient-low oxygen areas such as OMZs remove around three times as much N per unit of C deposited as sediments underlying highly oxygenated water, and account for approximately 10% (i.e. 0.001 Pmol N yr^{-1}) of global benthic denitrification (Bohlen et al., 2012). The amount of this loss is significant in regards to the inventory of fixed N (~ 300 Pmol,) and if not compensated for by other sources, has the potential to affect the content of bioavailable N over a time scale of ~10 000 yrs (Gruber, 2016). It is not yet known whether the recently inferred quadrupling of oxygen-deficient waters (Schmidtko et al., 2017) has been accompanied by a corresponding increase in anaerobic remineralization and denitrification. In oxic conditions, Fe and P can be adsorbed on particles in the sediment and onto sinking marine aggregates. With the onset of oxygen deficient conditions, the P bound to Fe oxides is generally remobilized and released to the overlying water, where it has the potential to stimulate primary production and hence further the oxygen deficiency. Oxygen deficient regions are enriched in iron and, based on the Redfield ratio, have an excess of P relative to N. These conditions are expected to be favourable for the fixation of N_2 by photosynthetic bacteria (e.g. *Prochloroccocus*, *Synechococcus*) that produce fixed N and that can potentially compensate for the loss of fixed N by denitrification and anammox. The feedbacks that link N loss and N fixation remain enigmatic. It is not yet known whether, on what time scales and to what extent global rates of N fixation respond to changes in N loss processes that are likely associated with ongoing deoxygenation (Deutsch et al., 2007; Knapp et al., 2016; Landolfi et al., 2013).

1.4.4.2 Impact on living organisms

At 100% saturation, the amount of oxygen available in one litre of water is ~35 times less than that in an equivalent volume of air. This means that in order for a marine animal to extract the same amount of oxygen in support of metabolism, the organism must pass 35 times more volume of medium across their gas exchange surfaces (gills vs lungs) or have to be much more efficient in taking up oxygen than terrestrial organisms. Critical physiological processes like respiration depend on the flux of oxygen into marine organisms (Seibel, 2011). This flux is governed by the gradient in oxygen partial pressure (pO_2) across membranes and tissues. Because pO_2 incorporates the effects of temperature, salinity and hydrostatic pressure into one single number, pO_2 thresholds are expected to be universally applicable (Hofmann et al., 2011; Seibel, 2011). Currently, most of the experiments (e.g. Davidson et al., 2016; Stevens & Gobler, 2018; Vasquer & Duarte, 2008) have addressed the effect of O_2 concentrations (rather than pO_2) on living organisms. An absolute pO_2 threshold below

which aerobic life is not sustainable still remains to be determined.

Contrary to pO_2, oxygen concentrations do not incorporate the effect of temperature, salinity and hydrostatic pressure. Consequently, species living in open ocean permanent OMZs do not have the same oxygen concentration thresholds as species experiencing seasonal oxygen depletion in the warmer coastal ecosystems (Hofmann et al., 2011). Nevertheless, a comparative analysis of experimentally derived oxygen concentration thresholds for benthic organisms shows that there is no one single oxygen concentration threshold but rather that this threshold value can exhibit significant variability when viewed across the high diversity of taxa found in the oceans. This analysis predicts that, as oxygen declines, the sequence of losses of benthic fauna during a low oxygen event should be initiated by the loss of fish, followed by crustaceans, then worms, echinoderms, and molluscs (Vasquer & Duarte, 2008).

These differences reflect differences in taxa traits describing their ability to adapt and to escape, such as mobility, life cycle dynamics, physiological tolerance, and metabolic adaptation over hours to days (e.g. reduced activity, lowered heartbeat rate, shift to anaerobic metabolism) (e.g. Vasquer & Duarte, 2008). Species inhabiting the permanent open ocean OMZs have evolved to be adapted to these low oxygen concentrations; an example is the vampire squid (Figure 1.9) living off California with oxygen levels below 15 µmol O_2 kg^{-1} (Seibel et al., 1999).

1.5 Ecosystem consequences: The challenge of scaling up from species to ecosystem

The development and extension of low oxygen areas degrade the living conditions and vertically contract the metabolically viable habitat for a large number of living species. It alters marine ecosystems and biogeochemical cycles by shifting the spatial distribution of species, altering trophic relationships by favouring low-oxygen tolerant species including invasive species and microbes, and excluding sensitive species with, in the case of severe oxygen deficiency, increased mortality of the most sensitive ones (Hofmann et al., 2011). Exposure of animals to low oxygen can induce movement (avoidance), reduce survival and growth, alter behaviour and prey-predator interactions, impair

Figure 1.9 Vampire squid, *Vampyroteuthis infernalis*, recovered from 700 m depth off the coast of southern California. This species possesses specific physiological adaptations that enable them to survive in the extreme, persistent hypoxia of the oxygen minimum layer. (Seibel et al., 1999, Photograph taken by B. Seibel).

reproduction, trigger epigenetic changes, disrupt life cycles, and cause mortality (Breitburg et al., 2018). Mobile species that have the capability to avoid low oxygen waters by swimming or crawling away may escape low oxygen conditions and accumulate in well oxygenated waters. They may become more vulnerable to fishers targeting these high oxygen refuge areas. Although short-term economic benefits may result, there is concern that these strategies can contribute to misinformed management, and potentially contribute to over-harvesting of affected stocks both in coastal areas (Craig & Bosman, 2013) and the open ocean (Stramma et al., 2012). For instance, observations show that the vertical expansion of the OMZs in the tropical north-east Atlantic restricts the migration depth of billfishes and tunas to a narrower surface layer, potentially increasing their vulnerability to surface fishing gear and distorting information used in fisheries management that could lead to over-harvesting (Stramma et al., 2012). This reduction of the migration depth of these fishes can be due to a reduction of their habitat or that of their prey due to the expansion of OMZs. In coastal areas, hypoxia modifies the structure of the benthos and may affect the bioturbating/bio-irrigating activities of the macrofauna with feedbacks on the biogeochemistry of the coastal waters that are not yet well understood.

The extrapolation to marine habitats of results from laboratory controlled-experiments is not direct for several reasons. For instance, the coastal LOZ is often associated with a high level of productivity (via eutrophication or upwelling) that can be beneficial for marine animals and partially compensate for the detrimental effects of low oxygen. Oxygen concentrations in the field are not constant but vary in response to potential intermittent mixing events, oxygen consumption and production from living communities. Multiple stressors like warming, deoxygenation and acidification can interact and generate synergistic or antagonistic effects that affect the isolation and detectability of oxygen effects (Vasquer & Duarte, 2008). Also, the description of the impact of low oxygen conditions at the scale of the ecosystem is mostly qualitative and speculative. The scaling-up of information obtained in the laboratory at species level to robust quantitative information at the level of the ecosystem (~ several hundreds of kilometres) requires the development of a suite of advanced methodologies. Data analysis and simulation models provide maps of oxygen values, and appropriate transfer functions have to be devised in order to translate the consequences of a LOZ on ecosystem functions. If appropriately parameterized, high trophic levels models can make the link with fisheries. For the biogeochemistry, some important parameterizations are still missing (e.g. N-fixation, N_2O pathways) as well as the impact of oxygen deficiencies on living organisms that mediate biogeochemical cycling (e.g. in the benthic ecosystem). The transfer of information on the environment provided by numerical models that basically address the low trophic levels up to the ecosystem faces several limitations. These include the limited capabilities of current models to simulate low oxygen values (< 20 µM), their rather coarse resolution (~ >1 km), the choice of the appropriate indicator of oxygen deficiency (concentration versus pO_2, duration of the event), the presence of other stressors (e.g. warming, acidification) that are expected to affect the lethal oxygen threshold (Vaquer-Sunyer & Duarte, 2008).

1.6 Ecosystem services consequences

Deoxygenation effects on ecosystem services are well documented in several areas and suggestive but not well quantified in many other possible pathways. This is partly due to the dynamic and localized aspects of deoxygenation, and also because of the difficulty in isolating oxygen effects from the effects of other co-varying stressors such as temperature and acidification. The challenges in isolating and quantifying the ecological effects of low oxygen (and consequently its effects on ecosystem services) should not be misinterpreted as all effects are small; effects of low oxygen can be important but hidden with other stressors and may be very important episodically.

Ecosystem services are typically divided into four categories: Provisioning (e.g. food, fresh water), Cultural (aesthetic, spiritual, education), Regulating (e.g. disease, biodiversity, water purification), and Supporting (e.g. productivity, nutrient cycling). Provisioning services have received significant attention to date, with a focus on deoxygenation effects on fisheries. Modelling analyses of fisheries demonstrate that in those situations when hypoxia alone may have small to moderate population-level effects on biomass of fish and shellfish available for harvest, the effects become large or amplified when hypoxia is combined with other stressors. A prevalent effect of deoxygenation is changes in fishing locations in response to fine-scale distribution changes due to hypoxia that affect the catchability and bio-economics of fishing. Catchabilities are relied upon for effective

fisheries management and not including their effects can result in ill-informed management analyses and incorrect harvesting advice.

Cultural services are an understudied area in ecosystem services in general. Spiritual, therapeutic, and aesthetic values remain difficult to quantify. One area of deoxygenation effects on cultural services is related to fisheries and is when deoxygenation, often in tandem with other stressors, affects traditional harvests of fish or shellfish used by indigenous peoples for spiritual purposes (Lynn et al., 2013). The potential for loss of valuable cultural services is illustrated by a recent bioeconomic analysis for the Chesapeake Bay. The loss was illustrated by showing the economic benefits that would result from improving water quality from today's conditions. The focus was on how management actions would lead to improved water quality that would result in increased recreational activities. Massey et al. (2017) roughly estimated that if the management targets on water quality were realized the benefits (in dollars) of improved water quality (including, but not limited to, higher oxygen) attributed to recreational use outside of fishing can be on the order of hundreds of millions of dollars annually. While this analysis is not a straightforward assessment of the impact of deoxygenation effects on cultural services, the results suggest that such assessments should be pursued.

The negative effects of deoxygenation on key regulating and supporting services continue to be areas of intense investigation. Alterations of benthic diversity and community structure (regulating services) due to low oxygen have been well documented (Diaz & Rosenberg, 2001; Levin et al., 2009). Another likely pathway is the loss of coral and seagrass cover due to low oxygen decreasing erosion control and water purification. How low oxygen affects the supporting services aspects of ecosystem services in terms of changes to biogeochemical cycling and the magnitude and food web pathways of productivity in coastal and open ocean ecosystems is becoming clearer but still further studies are required before generalizations can be made (Shepherd et al., 2017).

As ecology, economics, and social sciences continue to merge into integrated, coupled, natural and human systems analyses (Liu et al., 2007, 2015), the quantification of how deoxygenation and other environmental stressors affect ecosystem services will become more common.

1.7 Conclusions / Recommendations

Since about 1960, ocean deoxygenation has been occurring in the global and coastal ocean and is expected to worsen in a warming world with consequences for living organisms and on regional and global budgets of essential elements.

Better understanding of the deoxygenation process can be achieved by access to accurate observations and to furthering the reliability and coupling capabilities of physical, biogeochemical, plankton and benthic foodwebs, and upper trophic level models. Rapid advancement is being made in each of the modelling types, as well as in how best to couple them, in order to generate "climate to fish" models (Rose et al., 2010) that include oxygen effects. A regular monitoring of the state of the ocean with respect to oxygen based on observations and modelling offers new knowledge on the fundamental processes like global circulation, photosynthesis, respiration and interactions with the atmosphere. Keeling and Manning (2014) found that a better estimation of the oxygen air-sea flux would offer a better estimation of the Earth carbon budget of the order of 0.5 Pg C yr^{-1}. Indeed, the recent understanding that the air-sea flux of oxygen is probably not balanced, but rather reveals a net outgassing of oxygen from the ocean to the atmosphere leads to a revision of the global carbon budget and, in particular, the partitioning of the ocean and land carbon sinks.

Oxygen maps (climatologies) are regularly produced for the global ocean based essentially on ship-based data (e.g. Schmidtko et al., 2017; Stramma et al., 2008). Once quality checked, the oxygen time series delivered by Argo floats have the potential to enhance these climatologies by providing a high frequency signal. The lack of openly available oxygen data from the coastal ocean in a centralized database prevents a similar global mapping of oxygen for the coastal ocean. This would be needed in order to update the inventory of Diaz and Rosenberg (2008) and to reassess the state of deoxygenation in coastal waters.

The success of combating deoxygenation relies on our capacity to understand and anticipate its consequences in an environment affected by local, regional, and global processes. State-of-the-art models have capabilities to simulate the deoxygenation process in the global and coastal ocean, and their parameterizations and formulations should continuously evolve based on

new knowledge. Model development needs new observations and dedicated experiments, in particular in low oxygen and anoxic waters that are particularly challenging to measure and to model. Oxygen levels act as a "switch" for nutrient cycling and availability. The detailed nature of these thresholds and their ecological and biogeochemical implications are still a matter of intense scientific investigation.

For both the global and coastal ocean, an estimation of the uncertainty that accompanies projections of mean state is critical for management purposes. With this aim, ensemble approaches combining the projections of various models are promising, especially for the global ocean (e.g. Bopp et al., 2013); a similar process is emerging for the regional ocean as well (Meier et al., 2011). International platforms and programmes like IPCC (Intergovernmental Panel for Climate Change), IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services), the WCRP (World Climate Research Programme) CMIP (Coupled Model Intercomparison Project) project and the European Copernicus Marine Environment Service (CMEMS) promote the capacity to produce and evaluate ecological forecasts and long-term projections. Evidence has shown that the evolution of the oxygen levels is not a straightforward function of temperature but rather depends on the subtle interactions between physical and biogeochemical mechanisms whose balance can evolve in answer to anthropogenic forcings and over time scales of centuries (e.g. Jaccard & Gallbraith, 2012).

An enhanced understanding of the long-term response to climate warming of oxygen supply versus demand since the industrial revolution would improve our capabilities to project future changes (e.g. Deutsch et al., 2014).

A process that engages a dialogue between decision makers and scientists is necessary to foster communication between the two communities and to assure the saliency of model projections. Recently, IOC-UNESCO established the Global Ocean Oxygen Network (GO_2NE), a global network of ocean oxygen scientists, including experimentalists, modellers and field scientists, to promote scientific collaboration and public outreach (e.g. Breitburg et al., 2018).

1.8 References

Andrews, O.D., Bindoff, N.L., Halloran, P.R., Ilyina, T., & Le Quéré, C. (2013). Detecting an external influence on recent changes in oceanic oxygen using an optimal fingerprinting method. *Biogeosciences*, *10*, 1799-1813. https://doi.org/10.5194/bg-10-1799-2013

Armstrong, R. A., Lee, C., Hedges, J. I., Honjo, S., & Wakeham, S. G. (2002). A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep Sea Research Part II*: *Topical Studies in Oceanography, 49,* 219–236. https://doi.org/10.1016/S0967-0645(01)00101-1

Bachèlery, M.-L., Illig, S., & Dadou, I. (2015). Interannual variability in the South-East Atlantic Ocean, focusing on the Benguela Upwelling System: Remote versus local forcing. *Journal of Geophysical Research: Oceans*, *121*, 284–310. https://doi.org/10.1002/2015JC011168

Bange, H. (2006). Nitrous oxide and methane in European coastal waters. *Estuarine, Coastal and Shelf Science, 70,* 361-374. https://doi.org/10.1016/j.ecss.2006.05.042

Bettencourt, J.H., Lopez, C., Hernandez-Garcia, E., Montes, I., Sudre, J., Dewitte, B., … Garçon, V. (2015). Boundaries of the Peruvian oxygen minimum zone shaped by coherent mesoscale dynamics. *Nature Geoscience*, *8,* 937-940. https://doi.org/10.1038/ngeo2570

Bianchi, D., Dunne, J.P., Sarmiento, J. L., & Galbraith, E. D. (2012). Data-based estimates of suboxia, denitrification, and N_2O production in the ocean and their sensitivities to dissolved O_2. *Global Biogeochemical Cycles, 26*. https://doi.org/10.1029/2011GB004209

Billen, G., & Garnier, J. (2007). River basin nutrient delivery to the coastal sea: Assessing its potential to sustain new production of siliceous algae. *Marine Chemistry*, *106,* 148-160. https://doi.org/10.1016/j.marchem.2006.12.017

Bohlen, L. Dale, A. W., & Wallmann, K. (2012). Simple transfer functions for calculating benthic fixed nitrogen losses and C: N: P regeneration ratios in global biogeochemical models. *Global Biogeochemical Cycles*, 26. https://doi.org/10.1029/2011GB004198

Bopp, L., Le Quéré, C., Heimann, M., Manning, A. C., & Monfray, P. (2002). Climate-induced oceanic oxygen fluxes: Implications for the contemporary budget. *Global Biogeochemical Cycles*, *16*. https://doi.org/10.1029/2001GB001445

Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., … Vichi, M. (2013). Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences*, *10*, 6225-6245. https://doi.org/10.5194/bg-10-6225-2013

Brandt, P., Hormann, V., Körtzinger, A., Visbeck, M., Krahmann, G., & Stramma, L. (2010). Changes in the Ventilation of the Oxygen Minimum Zone of the Tropical North Atlantic. *Journal of Physical Oceanography, 40,* 1784–1801. https://doi.org/10.1175/2010JPO4301.1

Breitburg, D., Levin, L., Oschlies, A., Grégoire, M., Chavez, F., Conley, D., … Zhang, J. (2018). Declining oxygen in the global ocean

and coastal waters. *Science*, *359*, 10.1126/science.aam7240. https://doi.org/10.1126/science.aam7240

Cabré, A., Marinov, I., Bernardello, R., & Bianchi, D. (2015). Oxygen minimum zones in the tropical Pacific across CMIP5 models: mean state differences and climate change trends. *Biogeosciences*, *12*, 5429-5454. https://doi.org/10.5194/bg-12-5429-2015

Canfield, D., & Thamdrup, B. (2009). Towards a consistent classification scheme for geochemical environments, or, why we wish the term 'suboxic' would go away. *Geobiology*, *7*, 385–392. https://doi.org/10.1111/j.1472-4669.2009.00214.x

Capet, A., Stanev, E., Beckers, J.-M., Murray, J., & Grégoire, M. (2016). Decline of the Black Sea oxygen inventory. *Biogeosciences*, *13*, 1287-1297. https://doi.org/10.5194/bg-13-1287-2016

Capet, A., Beckers, J.M., & Grégoire, M. (2013). Drivers, mechanisms and long-term variability of seasonal hypoxia on the Black Sea northwestern shelf-is there any recovery after eutrophication? *Biogeosciences*, *10*, 3943-3962. https://doi.org/10.5194/bg-10-3943-2013

Conley, D.J., Paerl, H., Howarth, R.W., Boesch, D. F., Seitzinger, S.P., Havens, K., … Likens G.E. (2009). Controlling Eutrophication: Nitrogen and Phosphorus. *Science*, *323,* 1014-1015. https://doi.org/10.1126/science.1167755

Conley, D.J. (2012). Ecology: Save the Baltic Sea. *Nature*, *486*, 463–464. https://doi.org/10.1038/486463a

Craig, J. K., & Bosman, S.H. (2013). Small spatial scale variation in fish assemblage structure in the vicinity of the northwestern Gulf of Mexico hypoxic zone. *Estuaries and Coasts, 36*, 268-285. https://doi.org/10.1007/s12237-012-9577-9

Davidson, M., Targett, T., & Grecay, P. (2016). Evaluating the effects of diel-cycling hypoxia and pH on growth and survival of juvenile summer flounder *Paralichthys dentatus*. *Marine Ecology Progress Series*, *556*, 223-235. https://doi.org/10.3354/meps11817

Deutsch, C., Berelson, W., Thunell, R., Weber, T., Tems, C., McManus, J., … van Green, A. (2014). Centennial changes in North Pacific anoxia linked to tropical trade winds. *Science*, *345,* 665-668. https://doi.org/10.1126/science.1252332

Deutsch, C., Sarmiento, J.L., Sigman, D. M., Gruber, N., & Dunne, J.P. (2007). Spatial coupling of nitrogen inputs and losses in the ocean. *Nature*, *445*, 163-167. https://doi.org/10.1038/nature05392

Diaz, R., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*, *321*, 926-929. https://doi.org/10.1126/science.1156401

Diaz, R.J., & Rosenberg, R. (2001). Overview of Anthropogenically Induced Hypoxic Effects on Marine Benthic Fauna. In N.N. Rabalais, & R.E. Turner (Eds). *Coastal hypoxia: consequences for living resources and ecosystems*, Vol. 50, pp. 129-145, John Wiley & Sons. https://doi.org/10.1029/CE058p0129

Duarte, C.M., Conley, D.J., Carstensen, J., & Sánchez-Camacho, M. (2009). Return to Neverland: Shifting baselines affect eutrophication restoration targets. *Estuaries and Coasts, 32*, 29–36. https://doi.org/10.1007/s12237-008-9111-2

Duteil, O., Oschlies, A., & Böning, W. (2018). Pacific Decadal Oscillation and recent oxygen decline in the eastern tropical Pacific Ocean. *Biogeosciences*, *15*, 7111-7126. https://doi.org/10.5194/bg-15-7111-2018

Fennel, K., & Testa, J. (2018). Biogeochemical Controls on Coastal Hypoxia. *Annual Review of Marine Science, 11,* 105-130. https://doi.org/10.1146/annurev-marine-010318-095138

Frölicher, T. L., Joos, F., Plattner, G. -K., Steinacher, M., & Doney, S.C. (2009). Natural variability and anthropogenictrends in oceanic oxygen in a coupled carbon cycle–climate model ensemble. *Global Biogeochemical Cycles*, *23*, GB1003. https://doi.org/10.1029/2008GB003316

FDu, W., Primeau, F., Keith Moore, J., Lindsay, K., & Randerson, J.T. (2018). Reversal of increasing tropical ocean hypoxia trends with sustained climate warming. *Global Biogeochemical Cycles, 32*, 551-564. https://doi.org/10.1002/2017GB005788

Galloway, J.N., Leach, A.M., Bleeker, A., & Erisman, J.W. (2013). A chronology of human understanding of the nitrogen cycle. *Philosophical Transactions of the Royal Society London B Biological Sciences, 368,* 10.1098/rstb.20130120. https://doi.org/10.1098/rstb.2013.0120

Gray, J.S., Shiu-sun, R., & Or, Y.Y. (2002). Effects of hypoxia and organic enrichment on the coastal marine environment. *Marine Ecology Progress Series*, *238*, 249–279. https://doi.org/10.3354/meps238249

Gruber, N. (2016). Elusive marine nitrogen fixation. *Proceedings of the National Academy of Sciences of the United States of Americ*a, *113*, 4246-4248. https://doi.org/10.1073/pnas.1603646113

Hofmann, M., & Schellnhuber, H.-J. (2009). Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. *Proceedings of the National Academy of Sciences of the United States of America, 106,* 3017–3022. https://doi.org/10.1073/pnas.0813384106

Hofmann, A.F., Peltzer, E.T., Walz, P.M., & Brewer, P.G. (2011). Hypoxia by degrees: Establishing definitions for a changing ocean. *Deep Sea Research Part I: Oceanographic Research Papers, 58*, 1212-1236. https://doi.org/10.1016/j.dsr.2011.09.004

Holland, H.D. (2006). The oxygenation of the atmosphere and oceans. *Philosophical Transactions of the Royal Society London B Biological Sciences, 361*, 903-915. https://doi.org/10.1098/rstb.2006.1838

IPCC. (2013). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P.M. Midgley (Eds.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535.

Ito, T., Minobe, S., Long, M.C., & Deutsch, C. (2017). Upper ocean O_2 trends: 1958–2015. *Geophysical Research Letters, 44*, 4214–4223. https://doi.org/10.1002/2017GL073613

Jaccard, S.L., & Galbraith, E.D. (2012). Large climate driven changes of oceanic oxygen concentrations during the last deglaciation. *Nature Geoscience, 5*, 151-156. https://doi.org/10.1038/ngeo1352

Johnson, G. (2008). Quantifying Antarctic Bottom Water and North Atlantic Deep Water Volumes. *Journal of Geophysical Research*, *113*, C05027. https://doi.org/10.1029/2007JC004477

Karstensen, J., Stramma, L., & Visbeck, M. (2008). Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Progress in Oceanography*, *77*, 331 – 350. https://doi.org/10.1016/j.pocean.2007.05.009

Keeling, R., Körtzinger, A., & Gruber, N. (2010). Ocean deoxygenation in a warming world. *Annual Review of Marine Science, 2*, 199–229. https://doi.org/10.1146/annurev.marine.010908.163855

Keeling, R.F., & Manning, A.C. (2014). Studies of Recent Changes in Atmospheric O_2 Content. In K. Turekian, & H. Holland (Eds.) *Treatise on Geochemistry*: Second Edition, pp. 385-404. https://doi.org/10.1016/B978-0-08-095975-7.00420-4

Keeling, R.F., Najjar R.P., Bender, M., & Tans, P. (1993). What atmospheric oxygen measurements can tell us about the global carbon cycle? *Global Biogeochemical Cycles*, *7*, 37-67. https://doi.org/10.1029/92GB02733

Knapp, A.N., Casciotti, K.L. Berelson, W.M., Prokopenko, M.G., & Capone, D.G. (2016). Low rates of nitrogen fixation in eastern tropical south pacific surface waters. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 4398-4403. https://doi.org/10.1073/pnas.1515641113

Landolfi, A., Dietze, H., Koeve, W., & Oschlies, A. (2013). Overlooked runaway feedback in the marine nitrogen cycle: the vicious cycle. *Biogeosciences*, *10*, 1351–1363. https://doi.org/10.5194/bg-10-1351-2013

Kuenen, J.G. (2008). Anammox bacteria: from discovery to application. *Nature Reviews Microbiology*, *6*, 320-326. https://doi.org/10.1038/nrmicro1857

Le Quéré, C, Moriarty, R., Andrew, R.M., Canadell, J.G., Sitch, S., Korsbakken, J.I., … Zeng, N. (2015) Global Carbon Budget 2015. *Earth System Science Data*, *7*, 349-396. https://doi.org/10.5194/essd-7-349-2015

Levin, L.A., Ekau, W., Gooday, A.J., Jorissen, F., Middelburg, J.J., Naqvi, S.W.A., … Zhang, J. (2009). Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences, 6*, 2063-2098. https://doi.org/10.5194/bg-6-2063-2009

Libes, S. (1992). *An Introduction to Marine Biogeochemistry*. Wiley, New York, 734pp.

Liu, J., Dietz, T., Carpenter, S.R., Folke, C., Alberti, M., Redman, C.L., … Taylor, W.W. (2007). Coupled human and natural systems. *AMBIO*, *36*, 639-649. https://doi.org/10.1579/0044-7447(2007)36[639:CHANS]2.0.CO;2

Liu, J., Mooney, H., Hull, V., Davis, S.J., Gaskell, J., Hertel, T., … Li, S. (2015). Systems integration for global sustainability. *Science*, *347*, 963. https://doi.org/10.1126/science.1258832

Lynn, K., Daigle, J., Hoffman, J., Lake, F., Michelle, N., Ranco, D., … Williams, P. (2013). The impacts of climate change on tribal traditional foods. *Climatic Change*, *120*, 545-556. https://doi.org/10.1007/s10584-013-0736-1

Manning, A.C., & Keeling, R.F. (2006). Global oceanic and land biotic carbon sinks from the Scripps atmospheric oxygen flask sampling network. *Tellus*, *58B*, 95-116. https://doi.org/10.1111/j.1600-0889.2006.00175.x

Massey, D.M., Moore, C., Newbold, S.C., Ihde, T., & Townsend, H. (2017). Commercial fishing and outdoor recreation benefits of water quality improvements in the Chesapeake Bay. CEE Working Paper Series 2017-02, National Center for Environmental Economics, U.S. Environmental Protection Agency, revised Jul 2017.

Martinez-Rey, J., Bopp, L., Gehlen, M., Tagliabue, A., & Gruber, N. (2015). Projections of oceanic N_2O emissions in the 21st century using the IPSL Earth system model. *Biogeosciences, 12*, 4133 – 4148. https://doi.org/10.5194/bg-12-4133-2015

Meier, H.E.M., Andersson H.C., Eilola, K., Gustafsson, B.G., Kuznetsov, I., Müller-Karulis, B., … Savchuk, O.P. (2011). Hypoxia in future climates: a model ensemble study for the Baltic Sea. *Geophysical Research Letters, 38*, L24608. https://doi.org/10.1029/2011GL049929

Pascual, A., Ruiz, S., Olita, A., Troupin, C., Claret, M., Casas, B., … Tintoré, J. (2017). A Multiplatform Experiment to Unravel Meso- and Submesoscale Processes in an Intense Front (AlborEx). *Frontiers in Marine Science, 4*, 39. https://doi.org/10.3389/fmars.2017.00039

Piiper, J. (1982). Respiratory gas exchange at lungs, gills and tissues: mechanisms and adjustments. *Journal of Experimental Biology*, *100*, 5–22.

Rabalais, N., Diaz, R., Levin, L., Turner, R., Gilbert, D., & Zhang, J. (2010). Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences*, *7*, 585-619. https://doi.org/10.5194/bg-7-585-2010

Revsbech, N.P., Larsen, L.H., Gundersen, J., Dalsgaard, T., Ulloa, O., & Thamdrup, B. (2009). Determination of ultra-low oxygen concentrations in oxygen minimum zones by the STOX sensor. *Limnology and Oceanography: Methods, 7*, 371–381. https://doi.org/10.4319/lom.2009.7.371

Rose, K., Dubravko, J., Fennel, K., & Hetland, R. (2017). Numerical Modeling of Hypoxia and Its Effects: Synthesis and Going Forward. In D. Justic, K.A. Rose, R.D. Hetland, & K. Fennel (Eds.) *Modeling Coastal Hypoxia,* Springer, pp. 401-421. https://doi.org/10.1007/978-3-319-54571-4_15

Rose, K.A., Allen, J.I., Artioli, Y., Barange, M., Blackford, J., Carlotti, F., … Zhou, M. (2010). End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps. *Marine and Coastal Fisheries*, *2*, 115-130. https://doi.org/10.1577/C09-059.1

Schmidtko, S., Stramma, L., & Visbeck, M. (2017). Decline in global oceanic oxygen content during the past five decades. *Nature, 542*, 335 - 339. https://doi.org/10.1038/nature21399

Seibel, B. (2011). Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *Journal of Experimental Biology*, *214*, 326 - 336. https://doi.org/10.1242/jeb.049171

Seibel, B.A., Chausson, F., Lallier, F., Childress, J.J., & Zal, F. (1999). Vampire blood: respiratory physiology of the Vampire Squid (Vampyromorpha: Cephalopoda) in relation to the oxygen minimum layer. *Experimental Biology Online*, *4*, https://doi.org/10.1007/s00898-999-0001-2

Seitzinger, S.P., Mayorga, E., Bouwman, A.F., Kroeze, C., Beusen, A.H.W., Billen, G., … Harrison, J.A. (2010). Global river nutrient export: A scenario analysis of past and future trends. *Global Biogeochemical Cycles*, *24*, GB0A08. https://doi.org/10.1029/2009GB003587

Shepherd, J.G., Brewer, P.G., Oschlies, A., & Watson, A.J. (2017). Ocean ventilation and deoxygenation in a warming world: introduction and overview. *Philosophical Transactions of the*

Royal Society A: Mathematical, Physical and Engineering Sciences, *375*. https://doi.org/10.1098/rsta.2017.0240

Somes, C.J., Oschlies, A., & Schmittner, A. (2013). Isotopic constraints on the pre-industrial oceanic nitrogen budget. *Biogeosciences*, *10*, 5889 – 5910. https://doi.org/10.5194/bg-10-5889-2013

Stevens, A., & Gobler, C. (2018). Interactive effects of acidification, hypoxia, and thermal stress on growth, respiration, and survival of four North Atlantic bivalves. *Marine Ecology Progress Series*, *604*, 143-161. https://doi.org/10.3354/meps12725

Stramma, L., Johnson, G.C., Sprintall, J., & Mohrholz, V. (2008). Expanding oxygen-minimum zones in the tropical oceans. *Science*, *320*, 655 - 658. https://doi.org/10.1126/science.1153847

Stramma, L., Schmidtko, S., Levin, L.A., & Johnson, G.C. (2010). Ocean oxygen minima expansions and their biological impacts. *Deep Sea Research Part I: Oceanographic Research Papers, 57*, 587 - 595. https://doi.org/10.1016/j.dsr.2010.01.005

Stramma, L., Prince, E.D., Schmidtko, S., Luo, J., Hoolihan, J.P., Visbeck, M., … Körtzinger, A. (2012). Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change*, *2*, 33-37. https://doi.org/10.1038/nclimate1304

Talley, L.D. (1993). Distribution and Formation of North Pacific Intermediate Water. *Journal of Physical Oceanography, 23*, 517–537. https://doi.org/10.1175/1520-0485(1993)023<0517:DAFONP>2.0.CO;2

Tiano, L., Garcia-Robledo, E., Dalsgaard, T., Devol, A.H., Ward, B.B., Ulloa, O., … Revsbech, N.P. (2014). Oxygen distribution and aerobic respiration in the north and south eastern tropical Pacific oxygen minimum zones. *Deep Sea Research Part I: Oceanographic Research Papers*, *94*, 173-183. https://doi.org/10.1016/j.dsr.2014.10.001

Vaquer-Sunyer, R., & Duarte, C.M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 15452 - 15457. https://doi.org/10.1073/pnas.0803833105

Wallmann, K. (2000). Phosphorus imbalance in the global ocean? *Global Biogeochemical Cycles*, *24*, GB4030. https://doi.org/10.1029/2009GB003643

Watson, A.J. (2016). Oceans on the edge of anoxia. *Science*, *354*, 1529 - 1530. https://doi.org/10.1126/science.aaj2321

Watson, A.J., Lenton, T.M., & Mills, B.J.W. (2017) Ocean deoxygenation, the global phosphorus cycle and the possibility of human-caused large-scale ocean anoxia. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *375*. https://doi.org/10.1098/rsta.2016.0318

Wright, J.J., Konwar, K.M., & Hallam, S.J. (2012). Microbial ecology of expanding oxygen minimum zones. *Nature Reviews Microbiology*, *10*, 381-394. https://doi.org/10.1038/nrmicro2778

"The decline in the oceanic oxygen content can affect ocean nutrient cycles and the marine habitat, with potentially detrimental consequences for fisheries, ecosystems and coastal economies."

Chapter 2.1 authors